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Comparative osteology of Malagasy poison frogs of the genus *Mantella* (Amphibia: Ranidae: Mantellinae)

Miguel Vences, Frank Glaw, Patrick Mausfeld & Wolfgang Böhme

Abstract. Osteological features of all 13 valid species of the anuran genus *Mantella*, as well as three unnamed forms, were studied in order to assess intragenetic phylogeny and to find support for the monophyletic status of *Mantella*. Two characters present in all species (lack of maxillary teeth and a reduced zygomatic squamosal process) support the monophyly of the genus. A third character (anterior hyale process forming a complete arch) was found to be individually variable but presumably also constitutes a autapomorphy of *Mantella*. Four characters were found to be variable between but relatively constant within species: sternum shape, nasal and sphenethmoid size, and shape of anterior parasphenoid process. A cladistic analysis of the observed character states resulted in *Mantella laevigata* and the *M. betsileo* group representing the most basal lineages within the genus. All other species constitute a monophyletic group characterized by a large sphenethmoid and widely separated nasals; from this main lineage a second, monophyletic group splits off. It is characterized by an unforked sternum and contains *M. nigricans*, *M. haraldmeieri*, *M. baroni*, *M. aff. baroni*, *M. cowani* and *M. bernhardi*. This phylogeny is largely in agreement with available data on mating calls and colour pattern.

Key words. Amphibia, Ranidae, Mantellinae, *Mantella*, osteology, phylogeny.

Introduction

Frogs of the genus *Mantella* are among the most prominent Malagasy amphibians. Due to their colourful pattern and their diurnal activity they are often kept in captivity.

Mantella is the type genus of the Mantellinae which is considered to be a subfamily of the Ranidae (Blommers-Schlösser 1993). Phylogenetic relationships of the Mantellinae within the framework of ranoid families and subfamilies have long been controversial. The most recent analysis of Blommers-Schlösser (1993) considered the Mantellinae as sister-group of the Rhacophorinae. No phylogenetic analysis of the position of *Mantella* within the subfamily Mantellinae exists, and intragenetic relationships have not been studied up to now (see Daly et al. 1996).

Mantella species are morphologically very similar to each other, and species diagnoses have mostly been based on colour patterns (Guibé 1964; Busse 1981). Bioacoustic data have only recently been used to discriminate species (e. g. Vences et al. 1994). The osteological diagnosis of *Mantella* as given by Blommers-Schlösser & Blanc (1991) is largely based on Guibé's (1978) study. Unfortunately, Guibé did not mention voucher specimens on which his results were based; he only published drawings of skull, shoulder girdle and hyoid apparatus of one specimen he attributed to *Mantella cowani*, and of the hyoid apparatus of *M. aurantiaca*. Blommers-Schlösser (1993) examined the osteology of *Mantella aurantiaca* in a broader context, but gave no additional data.

In the present study we analysed the osteology of all known species of the genus. Our aim was on (1) to identify characters shared by all species to find support for the monophyly of the genus. (2) we searched for characters which were consistent within but different between species, in order to analyse intrageneric relationships.

Material and methods

Specimens were skinned and their intestines removed as far as possible. A few specimens were partially cleared in KOH and stained for bones only in alizarin red. The remaining specimens were stained for bones and cartilage with alizarin red and alcian blue following the method of Dingerkus & Uhler (1977) with some minor modifications (Plösch 1991; Vences 1996). The flesh of many *Mantella* species was dark grey to blackish and did not clear to transparency; a better clearing was achieved in these cases by a high concentration of H_2O_2 in the first clearing steps.

The study was performed in the framework of a M. Sc. (=Diplom) thesis of the senior author (Vences 1996) which also contains a taxonomic revision of the genus *Mantella*. This revision will be published elsewhere; here we already apply the taxonomic changes which will be proposed in that publication. Differences to the accounts in Glaw & Vences (1994) are the use of the name *M. baroni* for the form previously named *M. madagascariensis* (see also Daly et al. 1996); the use of the name *M. madagascariensis* for the form previously named *M. "loppei"*; and the use of the name *M. nigricans* for specimens from the Marojezy mountains previously considered as *M. madagascariensis*. Specimens from a population with very variable colour patterns from the Andringitra mountains (Pic Ivohibe) are here named *M. aff. baroni*; their status pends further study. This is also true for specimens from Ankarana similar to *M. betsileo* (see Vences et al. 1996) which are here named *Mantella* sp. 1, and specimens similar to *M. aurantiaca* but with a black earspot which are here named *M. sp. 3*.

Studied specimens are deposited in the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK) and the Muséum National d'Histoire Naturelle, Paris (MNHN). The following 45 specimens were cleared and stained for osteological studies (* = stained for bones only; specimens without locality were supplied by the pet trade): *M. aurantiaca* (ZFMK 22113, ZFMK 22115*, ZFMK 22119 [juv.]); *M. baroni* (ZFMK 46035, ZFMK 48055* [Marolamba], ZFMK 62718–62721); *M. aff. baroni* (MNHN 1972–773, MNHN 1972–774 [both Col Ivohibe, Marovitsika forest]); *M. bernhardi* (ZFMK 62697–62698); *M. betsileo* (ZFMK 46004* [Nosy Boraha], ZFMK 62685–62687); *M. cowani* (ZFMK 62726); *M. crocea* (ZFMK 52746*, ZFMK 62767–62769); *M. expectata* (ZFMK 62716–62717); *M. haraldmeieri* (ZFMK 52741* [Nahampoana], MNHN 1973–508 [Chaines Anosyennes, Camp IV, Ambana], MNHN 1973–520 [Chaines Anosyennes, Camp IV and Ilibis]); *M. laevigata* (ZFMK 52749* [Nosy Mangabe], MNHN 1973–535 [Marojezy, 300 m]); *M. madagascariensis* (ZFMK 14186* [Niagarakely], ZFMK 14188 [Niagarakely], ZFMK 14196 [Niagarakely], ZFMK 62740–62741); *M. nigricans* (MNHN 1973–532, MNHN 1973–552 [both Marojezy, 600 m]); *M. pulchra* (ZFMK 56155*, ZFMK 62742–62744); *M. viridis* (ZFMK 48048*, ZFMK 62708–62709); *M. sp. 1* (ZFMK 61241* [Ankarana]); *M. sp. 3* (ZFMK 62770).

Due to differences in staining intensity and clearing, some characters could not be studied in all individuals. Other characters were only verified in one specimen of each species. Except for dorsal skull elements and shoulder girdle, which were studied in all stained individuals, our data refer to the following specimens (a buccal roof characters, b phalangeal characters, c hyoidal characters): ZFMK 14188 (c), 14196 (a, b, c), 22115 (b), 46004 (a, b), 46035 (b), 48055 (c), 52741 (b), 52746 (b), 61241 (b), 62685 (c), 62686 (c), 62687 (a, c), 62697 (a, b), 62698 (a, c), 62708 (a), 62709 (a, b), 62716 (a, b), 62717 (a, c), 62718 (c), 62719 (c), 62720 (c), 62721 (c), 62726 (a, b), 62740 (a, c), 62741 (c), 62744 (a, b), 62767 (c), 62768 (a), 62769 (a, c), 62770 (a, b); MNHN 1972–773 (a, b), 1972–774 (a, b), 1973–508 (a, b), 1973–520 (a, b), 1973–535 (a, b), 1973–532 (a, b, c), 1973–552 (a, b).

A cladistic analysis of the data was performed with Hennig86 software (Farris 1988). A strict consensus tree was constructed from the resulting equally parsimonious trees by using sequentially the commands mhennig*, bb* and nelsen.

Results

Drawings of the dorsal skull elements (mainly frontoparietals, sphenethmoid and nasals), shoulder girdle, and hyoid apparatus of some of the studied specimens are shown in figs. 1, 2 and 3, respectively. The following accounts shortly describe the states of the studied bone elements as observed in *Mantella*.

Intercalary element between terminal and subterminal phalanges of fingers and toes. — Present in all studied specimens and species. Always completely calcified in all fingers and toes.

Terminal phalanges of fingers and toes. — Guibé (1978) defined the terminal phalanges of *Mantella* as T-shaped, but he did not differentiate between T- and Y-shape (Blommers-Schlösser 1993). Generally, phalanges in specimens studied by us were distinctly Y-shaped at all fingers and toes. In some species the terminal bifurcation was less distinct (*M. aurantiaca*, *M. pulchra*). Interestingly, in at least one specimen of *M. laevigata* there was only a slight bifurcation at the terminal finger phalanges; no clear Y-shape was recognizable at toe phalanges, although *M. laevigata* is the *Mantella* species with the largest finger discs.

Omosternum. — This shoulder girdle element is completely ossified and widely forked in all studied *Mantella*. Some minor differences were noted in relative width of the proximal branches, but these were difficult to quantify.

Sternum. — The sternum of *Mantella* is always ossified and distinctly shorter than the omosternum. It was described as forked by Guibé (1978). In fact we observed a proximally forked sternum in most *Mantella*; however, *M. nigricans*, *M. haraldmeieri*, *M. baroni*, *M. aff. baroni*, *M. cowani* and *M. bernhardi* had always a clearly unforked sternum. This character seems generally not to be variable within species. Only in *M. crocea* we found a state in one specimen (unforked in ZFMK 52746) which differed from the state found in all other specimens (forked).

Squamosal. — This skull element has a distinct shape which we observed in all studied *Mantella* specimens, and which was already described by Guibé (1978). The anterior (zygomatic) process is very short, often only a reduced knob, whereas the posterior (otic) process is relatively long.

Frontoparietals. — These are the largest dorsal skull elements. They are more or less rectangular. The anterior edge of the complex of both frontoparietals is of a rounded, convex shape. In all sufficiently cleared and stained specimens it could be recognized that the two frontoparietals were medially separated from each other along their whole length.

Sphenethmoid. — Described by Guibé (1978) as “grand, envahissant la capsule olfactive”. We observed, however, a significant variation in size and shape of this element. In most species it is dorsally a relatively large undivided element which fills the gap between frontoparietals and nasals, largely overlapping with the former and slightly overlapping with the latter. Ventrally the sphenethmoid appears as a single large element that extends on the largest part of the buccal roof and distinctly overlaps with the anterior parasphenoid process.

In several species (especially *M. haraldmeieri*, *M. baroni*, *M. aff. baroni* and *M. cowani*) the sphenethmoid is generally larger; dorsally it extends to the front up to about half the dorsal extension of nasals; ventrally it is continued as lateral downwards directed arches.

In other species the sphenethmoid is reduced to different degrees. In *M. bernhardi* it dorsally does not get in contact with nasals (this, however, is mainly caused by the reduced nasal size); ventrally it still is one single element, but anteriorly it abruptly terminates along a straight line. In *M. betsileo*, *M. sp. 1* and *M. laevigata* it is dorsally relatively small, mostly

not overlapping with nasals, but ventrally it is reduced, either U-shaped along the parasphenoid process or a divided structure with two parts, respectively left and right of the parasphenoid. In *M. viridis* and *M. expectata* it is even more reduced, and occurs as small, divided structure both dorsally and ventrally.

Nasals. — We observed a significant variation in nasal size which is best quantified by the extension of the gap between both nasals. This gap is generally at least 30 % of the dorsally recognizable nasal width in most species (slightly less in *M. baroni*). In *M. bernhardi* and *M. madagascariensis* it is much larger, accounting for about 80 % in one *M. madagascariensis* (ZFMK 14188) and for more than 100 % in *M. bernhardi*. In *M. laevigata*, *M. expectata*, *M. viridis*, *M. sp. 1* and most *M. betsileo* the nasals are much closer to each other, nearly getting into contact in one *M. viridis* (ZFMK 62709).

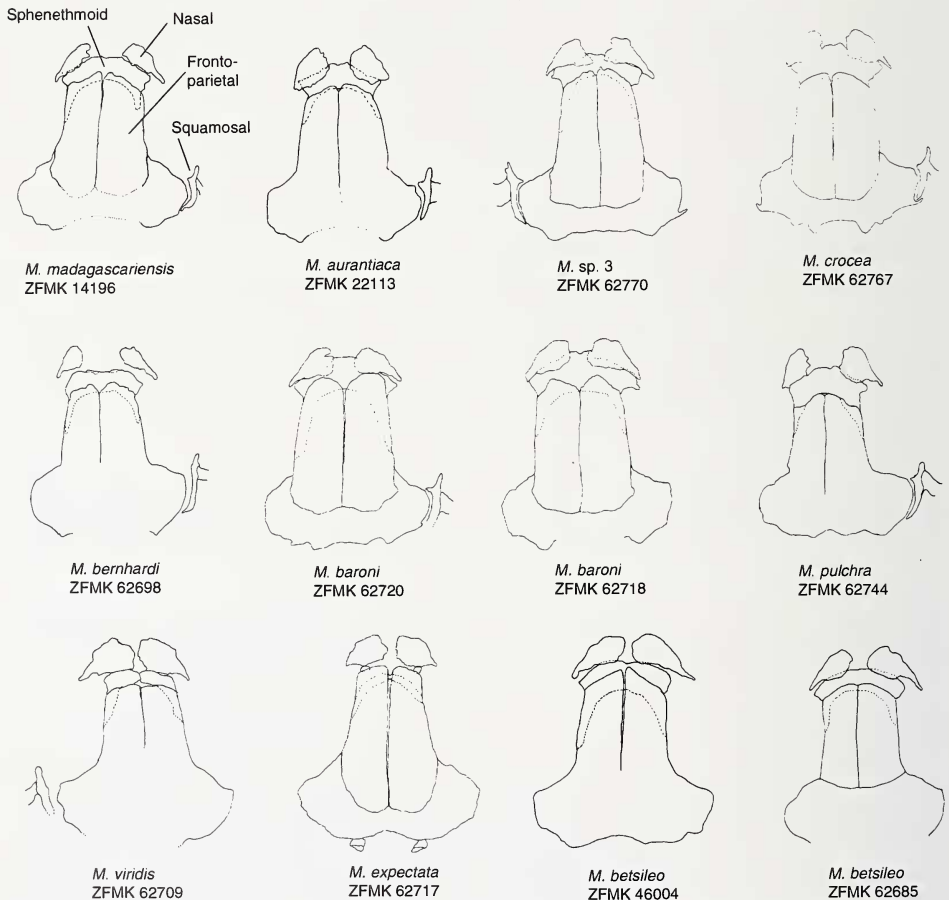


Fig. 1: Dorsal skull elements in several studied *Mantella* specimens. The drawings mainly focus on the different relative extension of nasals and sphenethmoid. Due to different degree of staining and clearing, posterior borders of frontoparietals and posterior skull elements were not recognizable in all specimens. Dashed line marks overlap of elements, stippled line marks parts which are not clearly recognizable. Drawings not to scale.

Maxilla. — In the specimens studied for buccal roof characters neither maxillary nor pre-maxillary teeth were observed. Guibé (1978) stated that there is no palatinal apophysis of the maxilla. In fact this dorsally directed process was very reduced in all studied specimens, but we generally observed rudiments.

Vomers. — The vomers were relatively small, thin, rectangular to ovoid plates. No vomerine teeth were present. Generally there were two short spine-like processes. There was a certain variation in vomer shape, some individuals having three to five processes (ZFMK 62770, 62726, MNHN 1972–774), and one specimen having remnants of a second element connected to the main vomerine element (MNHN 1973–552). However, these differences were also found intraspecifically, and we thus consider them as individual variation.

Palatines. — Described by Guibé (1978) as “assez reduites”. In all specimens examined by us the palatines appeared to be larger than in Guibé’s respective drawing. A certain variation in palatine size was observed, but it was difficult to quantify. However, in all species the palatines are relatively small; they neither reach the maxillae nor the parasphenoid.

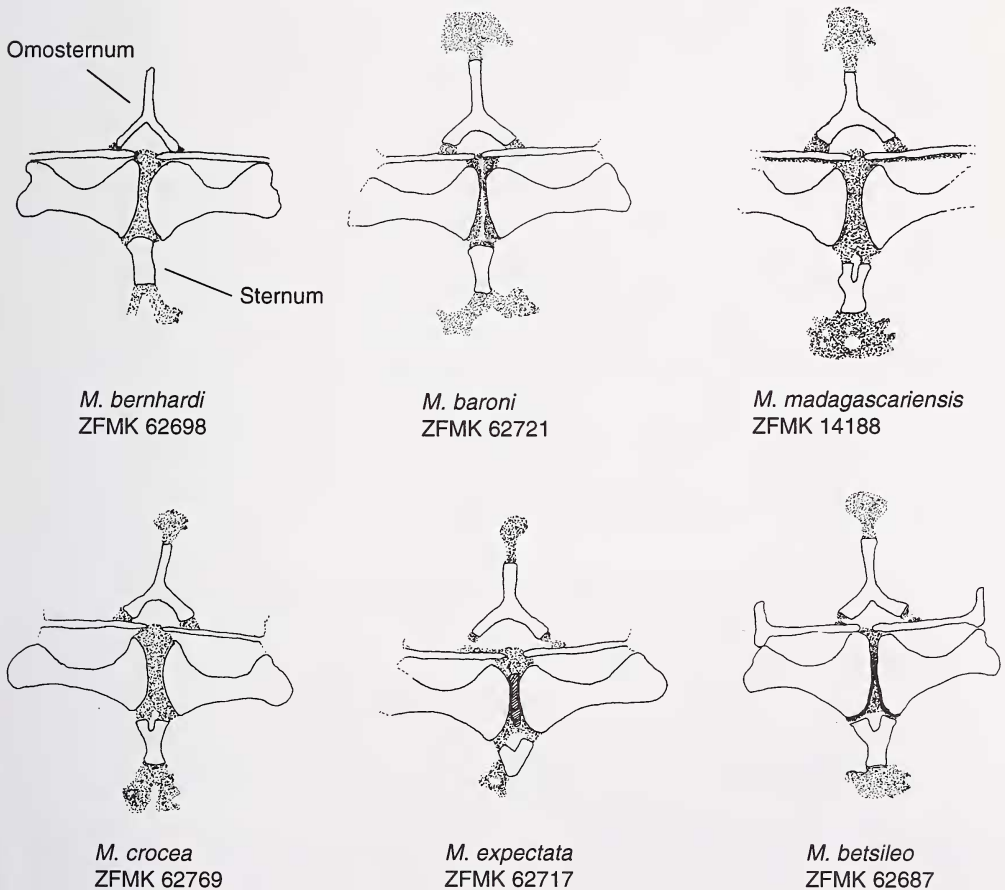


Fig. 2: Shoulder girdles in several studied *Mantella* specimens (ventral view). Note differences in sternum shape (forked/unforked). Cartilage elements stippled. Drawings not to scale.

Parasphenoid. — In most specimens only the anterior end of this element was examined. In most specimens the anterior edge had roughly a concave shape with a median notch (or several, irregular notches). This shape was poorly recognizable in *M. bernhardi* and some *M. madagascariensis* and *M. pulchra* (ZFMK 62740, 62744), and only slightly outlined in *M. viridis*. *M. haraldmeieri* and one *M. betsileo* (ZFMK 62687) had a straight end without notch. In both studied *M. expectata* it was not concave but convex, in ZFMK 62717 even rather sharply pointed.

Hyoid apparatus. — Due to different quality of alcian blue staining definitive statements on hyoid shape is not possible for all studied species. Structure of all visible hyoids is generally in accordance with the drawings of Guibé (1978) (relatively small anterolateral and a smaller

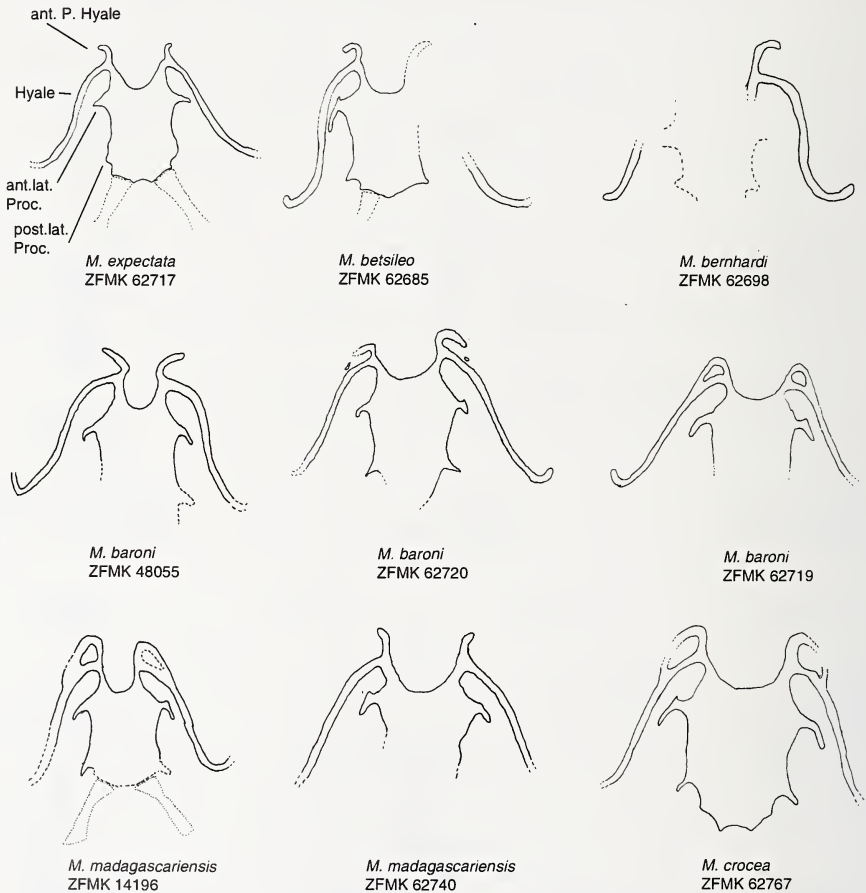


Fig. 3: Hyoid elements in several studied *Mantella* specimens (ventral view). Within two species (*M. madagascariensis* and *M. baroni*) both extreme hyale configurations (anterior process forming/not forming complete arch) were found. Abbreviations: ant. P. Hyale = anterior process of hyale; ant. lat. Proc. = anterolateral process; post. lat. Proc. = postero-lateral process. Stippled line marks parts which are not clearly recognizable. Drawings not to scale.

posterolateral process; slight hyoglossal sinus). However, we observed differences regarding the shape of the anterior process (anterior horn) of the hyale. In several specimens it was entire, forming a complete arch (see Drewes 1984: Character 11, state 0); in other specimens the lateral process of the anterior horn was absent (Drewes 1984: Character 11, state 2), with other specimens showing intermediate states. A complete arch was found in *M. aurantiaca* (see Guibé 1978), *M. baroni*, *M. nigricans*, *M. madagascariensis*, and *M. crocea*. Absence of the lateral process was noted in *M. expectata*, *M. betsileo*, *M. bernhardi*, *M. baroni*, and *M. madagascariensis*. Thus in at least two species (*M. baroni*, *M. madagascariensis*) the two extreme character states are known (see fig. 3). This variability does not seem to be correlated with sex. In females we found both entire horns (*M. nigricans*, MNHN 1973—532) and absent lateral processes (*M. madagascariensis*, ZFMK 62740; *M. bernhardi*, ZFMK 62698). In one probable male (*M. betsileo*, ZFMK 62685) the lateral process was absent.

Discussion

Monophyly of *Mantella*

Mantella are classified in the ranid subfamily Mantellinae together with the heterogeneous and large genus *Mantidactylus* which currently contains 59 species grouped in 12 subgenera according to Glaw & Vences (1994). The osteology of several *Mantidactylus* has been studied by Guibé (1978) and Blommers-Schlösser (1993). These authors used their data to describe the osteology of the genus in a generalized way. Detailed data for many species can be found only in Guibé's drawings. Additionally, we have own data regarding two species, *Mantidactylus luteus* and *M. blommersae*.

As far as known there are three osteological characters that can be used to distinguish *Mantella* from *Mantidactylus*: (1) All *Mantella* lack maxillary and premaxillary teeth which are present in *Mantidactylus*. (2) The squamosal of *Mantella* has a reduced zygomatic process; this structure is of variable relative length in *Mantidactylus*, but never as reduced as in *Mantella*. (3) *Mantella* have an anterior hyale process that forms a complete arch. Although this character seems to be individually variable, it is present in most examined *Mantella* but was never observed in *Mantidactylus*. According to Blommers-Schlösser (1993) the sister group of the Mantellinae is the Rhacophorinae. Using the Malagasy rhacophorine genus *Boophis* as outgroup, in all three above mentioned characters the states found in *Mantella* must be considered as derived and would thus support the monophyly of the genus. The large osteological homogeneity found in *Mantella* further corroborates that the genus is a monophyletic unit.

The use of *Boophis* as outgroup, however, must be seen with some caution. The placement of Rhacophorinae and Mantellinae as sister groups is based on only few characters (intercalary element, shape of terminal phalanges) which may not be as significant as previously thought (Glaw et al. 1998). An additional problem is that at least two of the synapomorphies of *Mantella* (squamosal shape and loss of teeth) may not be independent from each other but parts of a character complex related to microphagous specialization (Vences 1996). Despite these qualifications we conclude that all available data support the monophyly of *Mantella*. Even if the identified characters are not independent from each other they are still strong phylogenetic arguments.

Intrageneric relationships

Based on the results presented herein we consider four characters as suited for an intrageneric phylogenetic analysis. Variation in these characters is consistent within

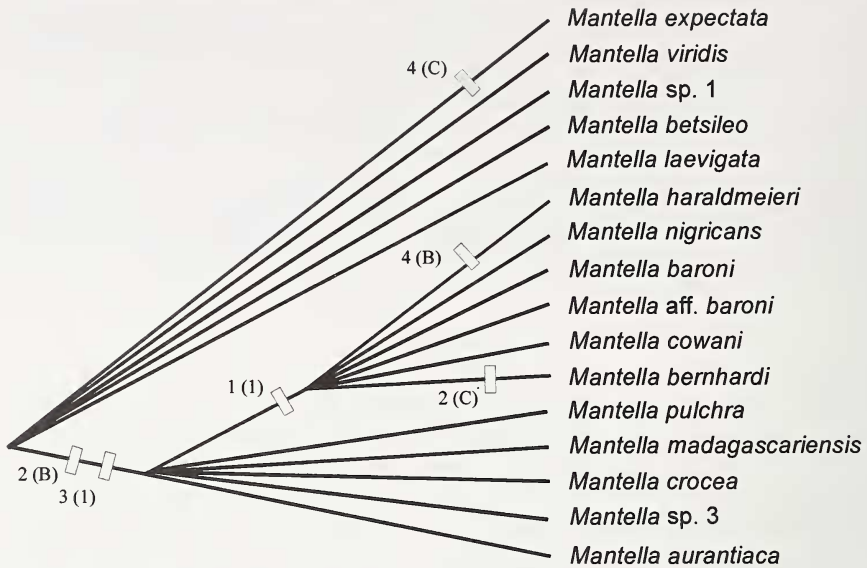


Fig. 4: Phylogeny of the genus *Mantella* as suggested by characters presented in table 1. Species in which different states were found were entered as follows in the analysis: *M. crocea*, character 1, state 0 (state 1 only found in one of four specimens). *M. betsileo*, character 2, state A (state B found in two of four specimens). *M. betsileo*, character 2, state A (state B found only in one specimen). Character 2 was entered as ordered transformation in the analysis, character 4 as unordered transformation. Length of the shown tree is 5 steps, consistency index and retention index is 100.

Table 1: Osteological character states in studied species of the genus *Mantella*. Explanation of characters and states is given in the discussion. Characters coded in arabic numbers were polarized by the outgroup method; 0 represents the plesiomorphic state. Characters coded in capital letters were not coded due to insufficient or contradictory outgroup data.

Species	Character 1	Character 2	Character 3	Character 4
<i>M. laevigata</i>	0	A	0	A
<i>M. betsileo</i>	0	A/B	0	A/B
<i>M. sp. 1</i>	0	A	0	?
<i>M. viridis</i>	0	A	0	A
<i>M. expectata</i>	0	A	0	C
<i>M. nigricans</i>	1	B	1	A
<i>M. haraldmeiri</i>	1	B	1	B
<i>M. baroni</i>	1	B	1	A
<i>M. aff. baroni</i>	1	B	1	A
<i>M. cowani</i>	1	B	1	A
<i>M. bernhardi</i>	1	C	1	A
<i>M. madagascariensis</i>	0	B	1	A
<i>M. pulchra</i>	0	B	1	A
<i>M. aurantiaca</i>	0	B	1	A
<i>M. sp. 3</i>	0	B	1	A
<i>M. crocea</i>	0/1	B	1	A

and variable between species. For polarization of states of these four characters we use *Mantidactylus* species of the subgenera *Guibemantis*, *Blommersia*, and *Pandanu-sicola* which show several similarities to *Mantella* (Blommers-Schlösser & Blanc 1993); they may represent basal clades within *Mantidactylus* which have retained character states of the mantelline ancestor (Blommers-Schlösser & Blanc 1991). Data on osteology of these *Mantidactylus* are based on Guibé (1978), Blommers-Schlösser & Blanc (1991) regarding configuration of shoulder girdles of some species, and own data on *M. blommersae*.

Sternum shape (character 1). Most studied outgroup representatives have a forked sternum (*Mantidactylus pulcher*, *M. depressiceps*, *M. bertini*, *M. blommersae*). Only data on *M. wittei* are contradictory (forked according to Guibé 1978, unforked according to Blommers-Schlösser & Blanc 1991). States are therefore 0 (sternum forked), 1 (sternum unforked), transformation 0—>1.

Nasal size (character 2). Within the outgroup there are both widely separated (*Mantidactylus blommersae*) and narrowly separated nasals (*M. pulcher*). A polarization of this character is therefore difficult. We divide states as follows: A (nasals narrowly separated, gap between them generally less than 30 % of dorsally recognizable nasal width), B (nasals widely separated, generally 30 %—80 % of nasal width), C (nasals extremely separated and very small, gap more than 100 % of nasal width).

Sphenethmoid size (character 3). *Mantidactylus pulcher* has dorsally a relatively small sphenethmoid; in *M. blommersae* it is reduced and divided. Ventrally it is rather reduced in *M. blommersae* (no data for *M. pulcher*). A large sphenethmoid can therefore be regarded as derived. We distinguish the following two states: 0 (sphenethmoid dorsally small, generally not overlapping with nasals; ventrally reduced, either divided, U-shaped), 1 (sphenethmoid dorsally and ventrally a single large element; dorsally generally overlapping with nasals, ventrally overlapping with parasphenoid), transformation 0—>1.

Parasphenoid shape (character 4). There are no reliable outgroup data, and we consider this state difficult to polarize. We distinguish three states: A (anterior process of parasphenoid generally concave with median notch; this shape sometimes only very faintly recognizable), B (anterior process ending straight, truncate), C (anterior process ending convex, pointed).

The distribution of character states in the studied *Mantella* species is shown in tab. 1, whereas fig. 4 shows the result of a cladistic analysis of the data. Following the osteological cladogram, the most basal species are *M. laevisgata* and the species of the *M. betsileo* group as defined by Vences et al. (1996). These species share a call generally consisting of double click notes and the lack of red or orange ventral colour on hindlegs (also absent in *M. nigricans*). A monophyletic group is defined by sternum shape (character 1, state 1); all species of this group are also characterized by the exclusive feature of a call generally composed of single click notes (except *M. bernhardi*, which has a unique, quite divergent call; no data are disponible for *M. aff. baroni*). As a conclusion, osteology contributes an important data set to an integrative analysis of *Mantella* phylogeny as we will publish it in a forthcoming paper.

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Zusammenfassung

Wir untersuchten osteologische Merkmale aller validen Arten der Anurengattung *Mantella*, sowie dreier unbeschriebener Formen, um Hinweise auf die intragenerische Phylogenie zu erhalten und Argumente für einen monophyletischen Status der Gattung zu erhalten. Zwei bei allen Arten nachgewiesene Merkmale, Abwesenheit von Maxillarzähnen und Reduktion des zygomatischen Fortsatzes des Squamosum, begründen die Monophylie von *Mantella*. Ein drittes Merkmal, der Ringschluß des anterioren Fortsatzes des Hyale, war individuell variabel, dürfte aber dennoch eine Synapomorphie aller *Mantella*-Arten darstellen. Vier Merkmale waren innerhalb der Arten relativ konstant, aber zwischen den Arten variabel: Die Form des Sternum, die Ausdehnung von Nasalia und Sphenethmoid sowie die Form des anterioren Fortsatzes des Parasphenoids. Eine phylogenetische Analyse der gefundenen Merkmalszustände zeigt, daß *Mantella laevigata* und die *M. betsileo* Gruppe die basalsten Stammlinien innerhalb der Gattung darstellen. Alle übrigen Arten sind durch ein großes Sphenethmoid und relativ kleine Nasalia als monophyletische Gruppe definiert; von dieser Hauptlinie zweigt eine weitere monophyletische Gruppe ab, die durch ein ungegabeltes Sternum definiert ist und die Arten *M. nigricans*, *M. haraldmeieri*, *M. baroni*, *M. aff. baroni*, *M. cowani* und *M. bernhardi* enthält. Diese phylogenetische Hypothese stimmt weitgehend mit der Gruppierung überein, die von bioakustischen und Färbungsmerkmalen nahegelegt wird.

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Miguel Vences, Patrick Mausfeld, Wolfgang Böhme, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn; Frank Glaw, Zoologische Staatssammlung München, Münchhausenstraße 21, 81247 München.